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Report

Directing Eye Gaze Enhances Auditory Spatial Cue Discrimination

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Summary

The present study demonstrates, for the first time, a specific enhancement of auditory spatial cue discrimination due to eye gaze. Whereas the region of sharpest visual acuity, called the fovea, can be directed at will by moving one's eyes, auditory spatial information is derived primarily from head-related acoustic cues. Past auditory studies have found better discrimination in front of the head [1–3] but have not manipulated subjects' gaze, thus overlooking potential oculomotor influences. Electrophysiological studies have shown that the inferior colliculus, a critical auditory midbrain nucleus, shows visual and oculomotor responses [4–6] and modulations of auditory activity [7–9], and that auditory neurons in the superior colliculus show shifting receptive fields [10–13]. How the auditory system leverages this crossmodal information at the behavioral level remains unknown. Here we directed subjects' gaze (with an eccentric dot) or auditory attention (with lateralized noise) while they performed an auditory spatial cue discrimination task. We found that directing gaze toward a sound significantly enhances discrimination of both interaural level and time differences, whereas directing auditory spatial attention does not. These results show that oculomotor information variably enhances auditory spatial resolution even when the head remains stationary, revealing a distinct behavioral benefit possibly arising from auditory-oculomotor interactions at an earlier level of processing than previously demonstrated.

Results

When making judgments about an object, we generally rely on the most informative sensory cues available [14, 15]. For visible objects, the eyes are more spatially reliable than the ears. As a result, auditory localization is strongly biased by a coincident visual stimulus [16]. Additionally, gazing toward a visual stimulus biases sound localization away from the direction of gaze over short time periods [17, 18] and toward it over longer ones [19], suggesting multiple mechanisms by which eye position influences auditory localization. Previous studies, however, have focused on absolute tasks (locating a sound) instead of relative tasks (discriminating two sounds' locations) and did not measure acuity. The observed oculomotor-based realignments of auditory localization behavior could reasonably emerge at any stage of processing from brainstem to cortex. However, performance on relative spatial discrimination tasks has been linked to the acuity of midbrain spatial receptive fields in owls [20, 21]. Thus, gaze-driven improvements in auditory spatial cue discrimination could be linked to oculomotor modulation of subcortical coding of these cues observed in a number of studies [7, 9–13].

Here we determined whether directing gaze to an auditory target increases behavioral sensitivity to binaural cues in that direction. We presented 16 subjects (11 female, 5 male; age 23.9 ± 3.1 years [mean ± SD]; thresholds $\leq$ 20 dB hearing level at octave frequencies 250–8,000 Hz) with trials consisting of an auditory or visual primer followed by a probe comprising two brief noise bursts at slightly different perceived positions (i.e., differing binaural cue values; Figure 1A) in a two-alternative forced-choice task. Sounds were presented via insert earphones. Subjects reported whether the second probe noise burst was to the right or to the left of the first probe noise burst (i.e., discriminated their relative positions). One subject was removed due to abnormal binaural perception, yielding N = 15.

Typically, interaural level differences (ILDs) are more informative regarding azimuth at frequencies above ~3 kHz and interaural time differences (ITDs) below ~1.5 kHz. These binaural cues are extracted in auditory brainstem nuclei: ILDs in the lateral superior olive (LSO), and ITDs in the medial superior olive (MSO). Because oculomotor activity may influence these parallel pathways differently, we manipulated the cues independently, using octave-wide noise bursts in the relevant high-frequency (centered at 4 kHz) or low-frequency (500 Hz) ranges. This created a lateralized percept, but stimuli were generally not perceived to be externalized as they would have been using free-field presentation. Because ILD and ITD were separately manipulated (alternate cue set to 0), some subjects may have perceived conflicting cues. This possibility was mitigated by filtering the stimuli to the relevant frequency ranges; furthermore, any potential impact on discrimination was taken into account by the initial calibration for each subject (see below).

The ILD or ITD was set for each subject so that sounds were perceived to be centered (0° azimuth midpoint) or to the side (±25° midpoint), with offsets of 12.0 ± 5.0 dB for ILD and 231 ± 89 μs for ITD. The excluded subject gave unnaturally large ILD and ITD offsets (42 dB; 1,157 μs). ILD and ITD discrimination thresholds were determined for each subject (5.9 ± 1.3 dB; 217 ± 70 μs) at their measured offset; performance was tested at these values thereafter. These thresholds are larger than in previous studies, which may have resulted from differing stimulus parameters or subjects' inexperience in interaural discrimination tasks [22].

Each experimental block employed either visual or auditory primers lasting 800 ms followed by a 200 ms pause before the probe started. Visual primers were a white fixation dot subtending 0.85° (turning gray after 800 ms to allow maintained fixation). Auditory primers were noise lateralized by the complementary binaural cue in the complementary frequency band (e.g., high-frequency ILD primer preceded low-frequency ITD probe), to test for effects of directed auditory

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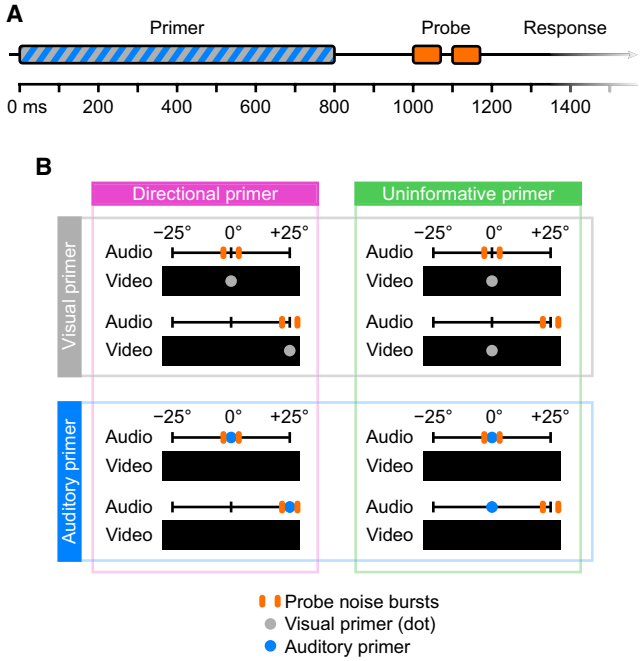

Figure 1. Stimulus Presentation and Blocking

(A) The time course of a trial. In visual trials, the dot brightened on fixation and darkened after 800 ms; in auditory trials, the primer was a noise burst. The probe noise bursts lasted 70 ms each, with 30 ms between each. The subject responded by button press any time after the stimulus. Primers provided the same timing information whether visual or auditory, directional or uninformative.

(B) Experimental blocks are shown one per quadrant. Each quadrant shows an example of a center trial above a side trial. The positions of the visual or auditory primers, where present, are shown as gray and blue dots, respectively. In auditory trials, subjects were presented with a black screen and not instructed where to direct their eyes. The probe noise bursts are shown as orange bars of different lateralizations centered about the primer.

See also Figure S1 for example eye gaze traces.

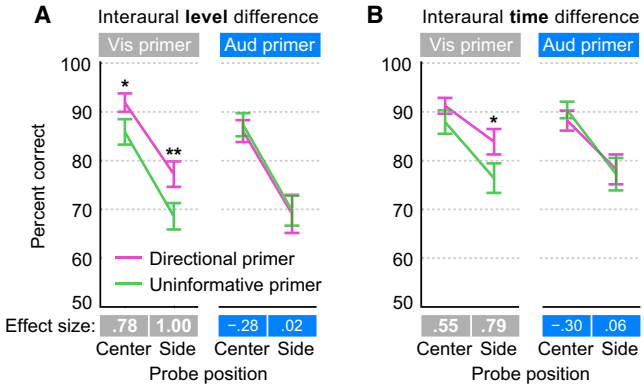

Figure 2. Directing Eye Gaze Improves Spatial Cue Discrimination

For interaural level difference (ILD, A) and interaural time difference (ITD, B) stimuli, the subject performance is shown for all conditions. Center performance was better than side performance. For ILD, performance was better in visual directional trials than in visual uninformative trials at both the center and side positions. For ITD, directional visual trials showed improved discrimination when the stimulus was located on the side. Auditory primers offered no benefit. Error bars indicate ±1 SEM (across the 15 intrasubject means). Asterisks indicate one-tailed paired t test significance: *p < 0.00625, **p < 0.00125 (Bonferroni-corrected values of 0.05 and 0.01, respectively). Effect size (within-subjects Cohen's d) of directional − uninformative contrast is bold where >0.5. Arcsine-transformed values were used for t tests and effect sizes; the means and error bars plotted are based on raw percent correct scores.

attention. Primers were either directional, indicating the midpoint lateralization of the impending probe, or uninformative, occurring in the center regardless of the probe's position. These variables resulted in four experimental blocks (Figure 1B). Fixation on visual primers was confirmed with eye tracking before each trial (see Figure S1 and Supplemental Experimental Procedures available online). The probe comprised two noise bursts lasting 70 ms each, with 30 ms between them. Subjects' gaze was not controlled in auditory trials, and they gazed near the center in the majority of trials.

Using four-factor within-subjects ANOVA, we found significant effects of probe position ($F(1,14) = 96.0$, $p = 1.2 \times 10^{-7}$), binaural cue type ($F(1,14) = 6.15$, $p = 0.026$), and an interaction between the two factors ($F(1,14) = 13.7$, $p = 0.0024$). Specifically, performance was better for center than for side probes (Figure 2), as expected [1–3]. Primer informativeness was significant ($F(1,14) = 4.75$, $p = 0.047$), but its interaction with primer modality was much more so ($F(1,14) = 20.5$, $p = 0.00048$), reflecting the fact that only directional visual primers improved performance. No other factors or interactions were significant. All statistics were performed on arcsine-transformed data.

The biggest improvement was due to gazing toward a side probe. Subjects benefitted from informative visual primers on both ILD ($p = 0.00083$, one-tailed paired t test, Bonferroni-corrected $\alpha = 0.00625$; Figures 2A and 3A, visual) and ITD trials ($p = 0.0044$; Figures 2B and 3B, visual). These results show that gazing toward an off-center stimulus enhances binaural discrimination, but could this come simply from knowing where to listen? Using an auditory primer instead of a visual one (meaning listeners were spatially primed but not directing gaze) provided no improvements ($p = 0.53$ ILD, $p = 0.41$ ITD). This result is surprising given that previous experiments have shown intelligibility benefits of knowing where to listen [23]. Those gains may come from facilitated selective attention, likely a cortical process [24]. The present results are consistent with a gaze-directed refinement of subcortical binaural cue coding.

Within one experimental block, all trials had either directional or uninformative primers. In trials with a central probe, directional visual primers improved discrimination for ILD probes ($p = 0.0051$). Auditory primers offered no benefit ($p \approx 0.9$ for ILD, ITD). Thus, while only knowing where to listen is not enough to improve discrimination, it does appear to affect whether a centered visual stimulus improves performance, at least for ILD-lateralized stimuli.

Discussion

Gaze-mediated modulations of auditory spatial processing have often been discussed in the context of bringing auditory information (innately head-centric) and visual information (innately eye-centric) into a common reference frame [9–12, 25]. However, as in vision, dynamically directing the region of highest auditory acuity (even if that region is broad, unlike the visual fovea) also likely has important behavioral benefits. When a listener attends to one speech stream while suppressing others, spatial separation between these sources increases intelligibility, an effect known as spatial release from masking that improves with increasing separations [26].

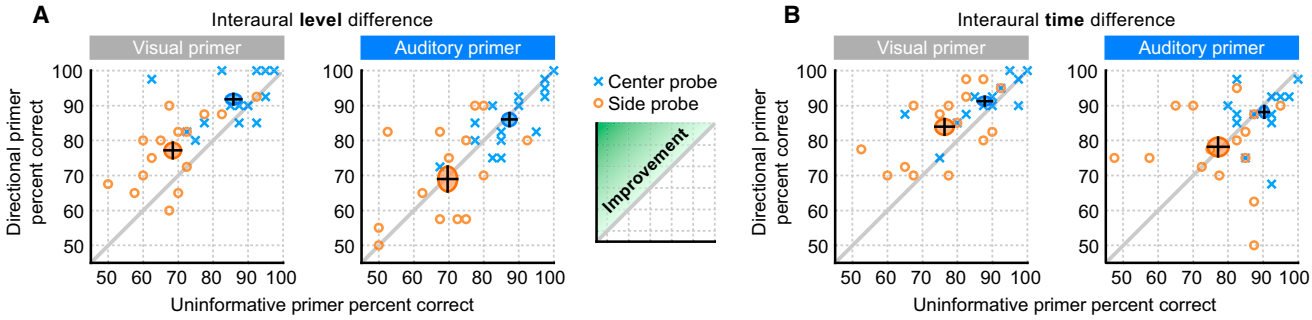

Figure 3. Most Subjects Show Improved Discrimination from Directing Eye Gaze

Directional primer performance is plotted against uninformative primer performance for each subject (N = 15). Panels are arranged and labeled as in Figure 2. Blue "X"s show individual subject mean performance on center-probe trials; orange "O"s show performance on side-probe trials. Centroids and SEM in each direction are shown as black crosses overlying colored ellipses whose radii are also defined by the SEM. Points in the upper left half of the plot show an improvement of the directional primer over the uninformative primer, points on the gray diagonal show no effect, and points below (in the lower right half) show a performance detriment. Note that in all four panels, center probe points and centroids (blue) are higher than side-probe points and centroids (orange), indicating that there was a marked improvement in discrimination of ILD and ITD in the center compared with the side.

(A) For ILD stimuli, most subjects show an improvement of the directional visual primer for both side and center probes, particularly for side probes. For auditory primers, performance is scattered evenly above and below, leading to centroids on the diagonal, showing no effect of a directional primer.

(B) Results are similar for ITD stimuli, although not significant for center probe trials.

Functionally speaking, improving spatial cue discrimination could effectively increase the perceptual separation (by decreasing the spatial ambiguity) of two sources that are physically close together. Studies of concurrent minimum audible angles (in which probe sounds were presented at the same time, rather than sequentially) [27, 28], the spatial acuity with which streams can be segregated [3], and the angles by which two sources need to be separated to be perceived distinctly [29] all suggest that there is indeed room for improvement when segregating lateral sound sources.

Over short periods of directed gaze, like those used here, shifts in the apparent sound-source location away from the direction of gaze have been demonstrated behaviorally [17, 18]. Unlike changes in acuity, such biases in perceived location could conceivably emerge at any level of processing, including in the cortex. However, it is worth speculating whether there is a physiological mechanism that could explain such shifts together with the discrimination enhancements of the current study (Figures 4A and 4C, centered gaze; Figures 4B and 4D, eccentric gaze).

Such a mechanism may arise from the fact that auditory brainstem spatial receptive fields are typically nonlinear, with many showing a transition zone between low and high spike rates where the slope is steepest. The best coding resolution, i.e., the most information, is found in this steeper region [30]. Intensity and ITD response functions have been shown to shift as result of adapting to stimulus statistics [31, 32]. Such shifts of nonlinear response functions change the operating point, resulting in larger differences in neural firing rates. Shifting rate-azimuth curves in the direction of eye gaze (Figures 4C and 4D, orange sound sources) is one mechanism that would allow the sound sources' locations to be better distinguished, improving discrimination (Figure 4B, orange circles more punctate than in Figure 4A). Moving the receptive field in this manner would predict that localization estimates would move opposite gaze direction to some degree, as has been observed previously [17, 18] (Figure 4, blue sources). For example, gazing leftward would shift the receptive field to the left, resulting in (1) better discrimination of the left-lateralized sounds, and (2) a rightward shift in the centered sound source's perceived azimuth (Figure 4D, blue arrow meeting perceived azimuth axis right of center). This shifting receptive field would not explain long-term localization biases in the same direction as gaze [19], but further investigation with varied timing may reconcile the present results with these findings. Furthermore, behavioral work has shown that gaze's interaction with sound localization is frequency dependent, implicating centers of the brain with tonotopic organization such as those in the ascending auditory pathway [33].

Gaze's effect on ILD discrimination may stem from such mechanisms. There is evidence of gaze-mediated shifts of auditory spatial receptive fields in superior colliculus (SC) and its avian analog [11–13]. The SC is the principal midbrain nucleus involved in executing saccadic eye movements and is thought to integrate spatial information across modalities [34]. It contains spatially tuned auditory neurons that typically respond to high frequencies and are generally more sensitive to ILDs [35, 36]. It is not clear whether these spatial receptive field shifts originate in SC, or whether they emerge in a previous level of processing, such as the external and pericentral nuclei of the inferior colliculus (IC) and the nucleus of the brachium of the IC, which project to SC [35, 37] or the superior olivary complex (which projects to IC [38]). In IC, gaze interacts in a complex way with auditory responses, producing a representation that is neither fully head- nor eye-centered but can be used to compute an eye-centric representation [7, 9]. Combinations of these responses, especially of units tuned to opposite azimuths, could result in shifting receptive fields downstream, which could in turn help to explain the improvements seen here in ILD discrimination for eccentric probes.

For ITD, a possible physiological mechanism for the improvements in discrimination may lie in the MSO, where ITD cues are calculated. Recordings in the MSO show that rate-ITD curves often peak outside the physiological range, with their region of maximal slope covering the relevant range [39]. Inhibition plays a role in ITD processing in the MSO [39], and while the details are debated, modulating this inhibition could shift ITD receptive fields [40]. It is conceivable that this modulatory signal could originate from nonauditory regions of the brainstem, midbrain, or cortex, although this is yet to be demonstrated. While not related to gaze, adaptive changes to ITD response functions observed in IC (which

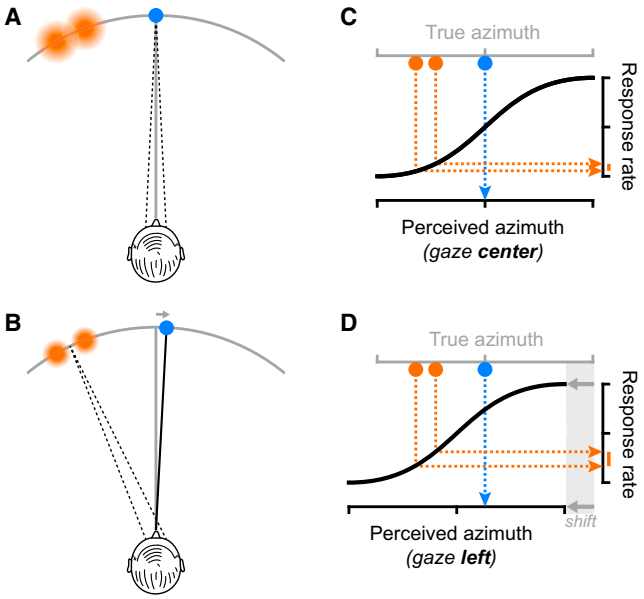

Figure 4. Behavioral Results Are Consistent with Shifting Spatial Receptive Fields

(A) When gaze is centered, there is some ambiguity in the difference between eccentric sources (blurred orange circles), and a centered sound is perceived correctly from the center (blue circle).

(B) When gaze is to the side, discrimination between eccentric sounds' positions increases (blur is reduced for orange circles), and the centered sound source is perceived as shifted in the direction opposite gaze (blue circle moved right).

(C) The unbiased spatial receptive field, plotting spike rate of a binaural neuron versus azimuth. Here, the true azimuth and the perceived azimuth are in alignment.

(D) The receptive field and perceptual azimuth axis have been shifted in the direction of gaze (left). This shift has two effects: (1) a larger difference between the neural firing rates from the eccentric targets (see orange bars on vertical axis), improving discrimination, and (2) the centered sound being right of center on the perceptual azimuth axis. The shift has been exaggerated for illustrative purposes.

receives MSO inputs [38]) indicate that such modulations are at least feasible [31].

What is driving these modulations of discrimination performance? The cortical network controlling visual attention is well studied [41], and the frontal eye field (FEF) region, an important node in this network, has strong connections to SC [42] as well as to the auditory cortex (AC) [43]. FEF is also important to auditory attention [44], and studies have shown sharpening of auditory spatial receptive fields by microstimulation in the avian FEF analog [13], suggesting a role in supramodal attention. Although AC is likely important to selective auditory attention [24], electrophysiological work has shown only weak effects of gaze in AC [7] compared with stronger modulations in IC [6, 9]. We posit that the improvement in discrimination observed here when directing gaze but not auditory attention alone results from modulation of subcortical auditory activity by the oculomotor, and even possibly the visual attentive system [45], independent of auditory attention.

Here we observed an enhancement in auditory spatial cue discrimination when gazing toward an auditory stimulus lateralized by manipulating either ILD or ITD. Crucially, discrimination saw no improvement in any experimental conditions where location was cued acoustically (leaving gaze undirected), demonstrating that simply knowing where to listen is not enough to improve discrimination, and that the oculomotor system is a necessary part of the observed enhancements. ILD discrimination also improved when the subject gazed toward a centered visual primer and knew the auditory probe would also be centered, suggesting that attention may affect gaze's impact on auditory spatial perception. Taken together, the results of this study are consistent with interaction of the oculomotor system with subcortical binaural processing pathways benefitting human spatial hearing.

Experimental Procedures

All methods were approved by the University of Washington Institutional Review Board. Acoustic stimuli were ramped on/off by a 10 ms $\cos^2$ envelope. Filtering was performed as frequency domain multiplication, yielding negligible energy outside passbands. There were 40 trials per data point per subject.

Individual ILD and ITD offsets were determined for each subject by aligning repeating acoustic noise bursts with a visual fixation dot at ±25° several times and averaging those estimates. We used a weighted up/down adaptive track to measure ILD and ITD discrimination at 75% performance at the center-gaze, side-probe condition, and these values separated probe bursts for the entire experiment. ITDs were applied to both envelope and fine structure.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.02.021.

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References

1. Mills, A.W. (1958). On the minimum audible angle. J. Acoust. Soc. Am. *30*, 237–246.
2. Hafter, E.R., De Maio, J., and Hellman, W.S. (1975). Difference thresholds for interaural delay. J. Acoust. Soc. Am. *57*, 181–187.
3. Middlebrooks, J.C., and Onsan, Z.A. (2012). Stream segregation with high spatial acuity. J. Acoust. Soc. Am. *132*, 3896–3911.
4. Porter, K.K., Metzger, R.R., and Groh, J.M. (2007). Visual- and saccade-related signals in the primate inferior colliculus. Proc. Natl. Acad. Sci. USA *104*, 17855–17860.
5. Bulkin, D.A., and Groh, J.M. (2012). Distribution of visual and saccade related information in the monkey inferior colliculus. Front. Neural Circuits *6*, 61.
6. Bulkin, D.A., and Groh, J.M. (2012). Distribution of eye position information in the monkey inferior colliculus. J. Neurophysiol. *107*, 785–795.
7. Maier, J.X., and Groh, J.M. (2010). Comparison of gain-like properties of eye position signals in inferior colliculus versus auditory cortex of primates. Front. Integr. Neurosci. *4*, 121.
8. Bergan, J.F., and Knudsen, E.I. (2009). Visual modulation of auditory responses in the owl inferior colliculus. J. Neurophysiol. *101*, 2924–2933.
9. Groh, J.M., Trause, A.S., Underhill, A.M., Clark, K.R., and Inati, S. (2001). Eye position influences auditory responses in primate inferior colliculus. Neuron *29*, 509–518.
10. Jay, M.F., and Sparks, D.L. (1984). Auditory receptive fields in primate superior colliculus shift with changes in eye position. Nature *309*, 345–347.

11. Jay, M.F., and Sparks, D.L. (1987). Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. J. Neurophysiol. *57*, 35–55.
12. Populin, L.C., Tollin, D.J., and Yin, T.C.T. (2004). Effect of eye position on saccades and neuronal responses to acoustic stimuli in the superior colliculus of the behaving cat. J. Neurophysiol. *92*, 2151–2167.
13. Winkowski, D.E., and Knudsen, E.I. (2006). Top-down gain control of the auditory space map by gaze control circuitry in the barn owl. Nature *439*, 336–339.
14. Talsma, D., Senkowski, D., Soto-Faraco, S., and Woldorff, M.G. (2010). The multifaceted interplay between attention and multisensory integration. Trends Cogn. Sci. *14*, 400–410.
15. Whitchurch, E.A., and Takahashi, T.T. (2006). Combined auditory and visual stimuli facilitate head saccades in the barn owl (*Tyto alba*). J. Neurophysiol. *96*, 730–745.
16. Recanzone, G.H. (2009). Interactions of auditory and visual stimuli in space and time. Hear. Res. *258*, 89–99.
17. Lewald, J. (1998). The effect of gaze eccentricity on perceived sound direction and its relation to visual localization. Hear. Res. *115*, 206–216.
18. Lewald, J., and Ehrenstein, W.H. (1996). The effect of eye position on auditory lateralization. Exp. Brain Res. *108*, 473–485.
19. Razavi, B., O'Neill, W.E., and Paige, G.D. (2007). Auditory spatial perception dynamically realigns with changing eye position. J. Neurosci. *27*, 10249–10258.
20. Bala, A.D.S., Spitzer, M.W., and Takahashi, T.T. (2003). Prediction of auditory spatial acuity from neural images on the owl's auditory space map. Nature *424*, 771–774.
21. Bala, A.D.S., Spitzer, M.W., and Takahashi, T.T. (2007). Auditory spatial acuity approximates the resolving power of space-specific neurons. PLoS ONE *2*, e675.
22. Wright, B.A., and Fitzgerald, M.B. (2001). Different patterns of human discrimination learning for two interaural cues to sound-source location. Proc. Natl. Acad. Sci. USA *98*, 12307–12312.
23. Best, V., Ozmeral, E.J., and Shinn-Cunningham, B.G. (2007). Visually-guided attention enhances target identification in a complex auditory scene. J. Assoc. Res. Otolaryngol. *8*, 294–304.
24. Mesgarani, N., and Chang, E.F. (2012). Selective cortical representation of attended speaker in multi-talker speech perception. Nature *485*, 233–236.
25. Lee, J., and Groh, J.M. (2012). Auditory signals evolve from hybrid- to eye-centered coordinates in the primate superior colliculus. J. Neurophysiol. *108*, 227–242.
26. Marrone, N., Mason, C.R., and Kidd, G. (2008). Tuning in the spatial dimension: evidence from a masked speech identification task. J. Acoust. Soc. Am. *124*, 1146–1158.
27. Perrott, D.R., and Saberi, K. (1990). Minimum audible angle thresholds for sources varying in both elevation and azimuth. J. Acoust. Soc. Am. *87*, 1728–1731.
28. Divenyi, P.L., and Oliver, S.K. (1989). Resolution of steady-state sounds in simulated auditory space. J. Acoust. Soc. Am. *85*, 2042–2052.
29. Best, V., van Schaik, A., and Carlile, S. (2004). Separation of concurrent broadband sound sources by human listeners. J. Acoust. Soc. Am. *115*, 324–336.
30. Harper, N.S., and McAlpine, D. (2004). Optimal neural population coding of an auditory spatial cue. Nature *430*, 682–686.
31. Maier, J.K., Hehrmann, P., Harper, N.S., Klump, G.M., Pressnitzer, D., and McAlpine, D. (2012). Adaptive coding is constrained to midline locations in a spatial listening task. J. Neurophysiol. *108*, 1856–1868.
32. Dean, I., Robinson, B.L., Harper, N.S., and McAlpine, D. (2008). Rapid neural adaptation to sound level statistics. J. Neurosci. *28*, 6430–6438.
33. Van Grootel, T.J., Van Wanrooij, M.M., and Van Opstal, A.J. (2011). Influence of static eye and head position on tone-evoked gaze shifts. J. Neurosci. *31*, 17496–17504.
34. Lewald, J., and Dörrscheidt, G.J. (1998). Spatial-tuning properties of auditory neurons in the optic tectum of the pigeon. Brain Res. *790*, 339–342.
35. Slee, S.J., and Young, E.D. (2013). Linear processing of interaural level difference underlies spatial tuning in the nucleus of the brachium of the inferior colliculus. J. Neurosci. *33*, 3891–3904.
36. Wise, L.Z., and Irvine, D.R. (1985). Topographic organization of interaural intensity difference sensitivity in deep layers of cat superior colliculus: implications for auditory spatial representation. J. Neurophysiol. *54*, 185–211.
37. Sparks, D.L., and Hartwich-Young, R. (1989). The deep layers of the superior colliculus. Rev. Oculomot. Res. *3*, 213–255.
38. Huffman, R.F., and Henson, O.W., Jr. (1990). The descending auditory pathway and acousticomotor systems: connections with the inferior colliculus. Brain Res. Brain Res. Rev. *15*, 295–323.
39. Pecka, M., Brand, A., Behrend, O., and Grothe, B. (2008). Interaural time difference processing in the mammalian medial superior olive: the role of glycinergic inhibition. J. Neurosci. *28*, 6914–6925.
40. Zhou, Y., Carney, L.H., and Colburn, H.S. (2005). A model for interaural time difference sensitivity in the medial superior olive: interaction of excitatory and inhibitory synaptic inputs, channel dynamics, and cellular morphology. J. Neurosci. *25*, 3046–3058.
41. Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. *3*, 201–215.
42. Leichnetz, G.R., Spencer, R.F., Hardy, S.G.P., and Astruc, J. (1981). The prefrontal corticotectal projection in the monkey; an anterograde and retrograde horseradish peroxidase study. Neuroscience *6*, 1023–1041.
43. Barbas, H., and Mesulam, M.-M. (1981). Organization of afferent input to subdivisions of area 8 in the rhesus monkey. J. Comp. Neurol. *200*, 407–431.
44. Lee, A.K.C., Rajaram, S., Xia, J., Bharadwaj, H., Larson, E., Hämäläinen, M.S., and Shinn-Cunningham, B.G. (2013). Auditory selective attention reveals preparatory activity in different cortical regions for selection based on source location and source pitch. Front. Neurosci. *6*, 190.
45. Müller, J.R., Philiastides, M.G., and Newsome, W.T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. Proc. Natl. Acad. Sci. USA *102*, 524–529.